Relationships between Standing Crops at Three Successive Trophic Levels in the Eastern Tropical Pacific[1]

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ABSTRACT: Measurements of the following standing crops were made at each of several pairs of stations on various cruises in the eastern tropical Pacific: (a) chlorophyll *a*, mg /m^2, 0–100 m; (b) zooplankton (total, and, for some cruises, copepods separately), ml/10^3m^3, 0–300 m; (c) small fish and cephalopods, combined, from net-caught micronekton, ml/10^3m^3, 0–90 m. These were considered to represent plants, herbivores, and primary carnivores. It was estimated that most of the zooplankton was located at 0–140 m. The stations of each station-pair were separated by less than 120 miles and 36 hr.

Relationships between the logarithms of crops were investigated by simple correlations, partial correlations, and structural two-variable linear regressions. In the 36 station-pairs available from cruises made in the northern spring, both zooplankton and carnivores had a significant positive regression on chlorophyll *a*; the points for 11 of these pairs fell within or close to the 95% confidence limits of each of the regressions. For these 11 "statistically selected" pairs all simple correlation coefficients were positive and significant, the partial correlation coefficient of chlorophyll *a* and zooplankton was positive and significant, and the other two partial correlation coefficients were non-significant. These results were considered to be consistent with steady-state conditions between the three standing crops. A similar analysis using copepods instead of total zooplankton gave a generally similar result. Chlorophyll *a* and primary productivity (by the C_{14} method) were positively and significantly correlated at 19 stations where both measurements were taken.

Most of the station-pairs for which these results were obtained were located in the area bounded by 5°N, 95°W, 12°N, and the American coast (excluding the Costa Rica Dome). This is a moderately eutrophic area, where a steady state might not have been expected; however, there are indications that the process of eutrophication, which probably is vertical mixing of the upper part of the very shoal thermocline (<30 m) by wind, is itself fairly steady throughout the year. No definite indications of a steady state were obtained from any other area at any season; however, the possibility of obtaining them from more copious material is not denied.

The regression (slope) coefficients showed that standing crop of herbivores varied as some power <1.0 of standing crop of chlorophyll *a*, suggesting increasingly inefficient utilization of plants by herbivores with increase of plant standing crop. On the other hand the crop of carnivores varied in an approximately linear way with that of herbivores. The standing crop ratios, copepods/plants (by weight of carbon) and carnivores/zooplankton (by displacement volume), were both roughly estimated at 0.04 under steady-state conditions; for various reasons the corresponding food-chain efficiency ratios, for standing crops of all material at the appropriate trophic levels, would be higher.

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SPEAKING OF THE SEA, Harvey (1955) said, "In nature an equilibrium between the standing crop of plants, herbivores and carnivores is continually passing in and out of balance." He clarified this statement by reference to temporary

excesses of material at some trophic levels being causally associated with temporary deficiencies at other levels, and in so doing he summarized much observation and interpretation of standing crop changes from many investigations in temperate and cold seas.

Recently a different concept, that of a virtually undisturbed balance between standing crops of biota, has been considered applicable to tropical ocean areas. For example, Nielsen (1958) said, "A direct relationship between phytoplankton and zooplankton is normal in the sea . . . with stable hydrographic conditions such as occur mainly in tropical and subtropical regions, the standing crop of phytoplankton and its production is stable"; Holmes (1958) spoke of "a situation approaching a steady state" in regard to relationships between standing crops of chlorophyll *a* and zooplankton in the eastern tropical Pacific; Cushing (1959*a, b*) distinguished two extreme types of productive cycle, one "unbalanced" (with the features noted by Harvey) in temperate and cold seas, the other "fully balanced" or in a "steady state" (with no change in standing crops) in non-upwelling tropical regions; Menzel and Ryther (1961) found phytoplankton production and zooplankton standing crop to be rather constant over most of the year and directly related over all of it, in the subtropical Sargasso Sea. None of these authors presented data on primary carnivores.

It is important to know where and when steady states occur because they are freely incorporated in analytical models of food-chain relations concerning various parts of the ocean (Riley, 1963). At the practical level they could be of use in making forecasts.

This paper deals with statistical analysis of measurements of standing crops of phytoplankton (as chlorophyll *a*), herbivores (as total zooplankton and, in part, as copepods), and primary carnivores (as micronektonic fish and cephalopods) which were all taken together at different times and places in tropical and subtropical parts of the eastern Pacific Ocean. The object of the study was to show for which (if any) of these time–space situations all standing crop measurements were consistent with a steady-state productive cycle. It was realized that such data could not prove the existence of such a cycle. It was necessary to make many of the measurements as opportunities offered, in the course of cruises undertaken for other purposes. The results of this work may encourage the making of additional much-needed observations of the same kind, or of better ones for the same purpose.

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MATERIAL: CRUISES, MEASUREMENTS, AND STATIONS

Cruises

Standing crops of chlorophyll *a*, zooplankton, and micronekton were measured frequently at oceanographic stations on eight cruises in tropical and subtropical parts of the eastern Pacific. On three of these cruises the observations were confined to a few small areas and do not serve the purpose of this study. The other cruises were those known as Scot (or TO–58–1) and TO–60–1, both made in the Northern Hemisphere and northern spring; Step-I (or TO–60–2), made in the Southern Hemisphere and southern spring; TO–59–1, in the Northern Hemisphere and northern winter; and TO–59–2, in the Northern Hemisphere and northern summer. Certain measurements made on these cruises were suitable for the present study in ways described below, and they are listed in Table 1.

Similar measurements of chlorophyll *a* and zooplankton, but not micronekton, were made on three other cruises, and those suitable for the present study are listed in Table 2. The cruises, known as Eastropic, Scope, and Costa Rica Dome, were all made in the Northern Hemisphere and northern autumn. Figure 1 shows the areas in which the measurements of Tables 1 and 2 were made.

TABLE 1

MEASUREMENTS OF STANDING CROPS OF CHLOROPHYLL *a* (mg/m^2), ZOOPLANKTON ($ml/10^3m^3$), CARNIVOROUS MICRONEKTON ($ml/10^3m^3$), AND COPEPODS ($ml/10^3m^3$), AT OCEANOGRAPHIC STATIONS (stns.) IN THE EASTERN TROPICAL PACIFIC*

STN. PAIR	NOON STN.	NIGHT STN.	NOON CHLOR.	NOON ZOOP.	NIGHT ZOOP.	G.M. ZOOP.	NIGHT MICRO.	NOON COP.	NIGHT COP.	G.M. COP.	NOTES
A. SCOT Expedition, 23 April–20 June, 1958											
1	4	3	9.7	23	24	23	2.6	0.36	1.51	0.73	
2	6	5	6.4	18	21	19	1.0	0.77	0.96	0.86	
3	8	7	14	10	20	14	3.3	0.51	0.89	0.67	
4	13	10	10	13	31	20	2.8	0.64	1.50	0.98	1
5	15	14	16	30	50	39	6.7	2.46	1.42	1.87	
6	23	27	13	79	57	67	1.0	1.89	4.52	2.92	2
7	28	29	12	49	67	57	4.4	1.67	1.94	1.80	
8	32	33	15	72	100	85	8.5	3.22	5.45	4.19	
9	34	35	12	85	84	84	4.0	7.00	6.75	6.87	
10	42	36	14	86	56	69	10.0	1.74	7.30	3.56	1
11	45	46	22	63	87	74	9.5	3.87	4.25	4.06	
12	47	48	46	100	163	131	13.9	7.85	15.06	10.87	
13	49	49	39	270	299	284	19.1	30.96	11.90	19.20	1
14	56	56	36	85	101	93	6.5	3.63	1.82	2.57	1
15	58	57	81	74	79	76	4.1	4.57	3.97	4.26	
16	60	59	41	113	148	129	7.5	5.28	3.05	4.01	
17	62	61	29	80	104	91	5.9	2.28	6.16	3.74	3
18	70	69	45	90	160	120	10.0	2.23	7.05	3.96	
19	72	71	39	130	150	140	7.9	6.63	5.49	6.03	
20	74	73	50	114	182	144	16.7	3.66	6.88	5.02	3
21	76	75	120	117	206	155	15.5	4.16	10.30	6.55	
22	79	77	49	74	111	91	24.5	0.85	6.12	2.28	
23	86	85	27	108	84	95	15.4	3.74	5.81	4.66	
24	88	90	26	127	143	135	12.7	5.77	4.26	4.96	
25	100	98	11	48	48	48	16.7	2.51	4.72	3.43	4, 5
26	122	118	23	107	122	114	13.8	6.31	7.38	6.82	5
27	139	135	37	44	52	48	14.5	2.61	4.68	3.49	5
B. TO–60–1 Expedition, 30 April–27 May, 1960											
1	20	18	11	37	77	53	1.1	1.08	5.63	2.47	
2	25	23	7.4	22	32	27	2.2	1.28	1.32	1.30	
3	31	33	6.0	56	50	53	5.5	2.72	3.70	3.17	
4	42	40	7.4	38	59	47	5.9	2.50	1.65	2.03	
5	46	44	4.8	61	63	62	4.0	1.45	2.82	2.02	
6	50	48	6.0	42	41	41	2.8	2.94	0.61	1.34	
7	54	52	9.3	68	57	62	6.8	1.42	2.68	1.95	
8	58	56	19	53	95	71	1.4	1.01	7.85	2.82	6
9	58	59	19	53	115	78	5.5	1.01	1.44	1.21	6

* In water columns or layers to about 100 m, 300 m, 90 m, and 300 m respectively, with exceptions noted; abbreviated as chlor., zoop., micro., and cop. respectively. G.M. means geometric mean. For further explanation see text and footnotes.

1. Noon and night station positions were identical.
2. No zooplankton haul was made at station 23; the value given is from an adjacent daytime station (25).
3. Micronekton net was slightly torn during the haul.
4. No zooplankton haul was made at station 98; the value given is from an adjacent night station (99).
5. Night zooplankton and night copepods were estimated as in Appendix I because the haul was shallow.
6. Same noon station was paired with two equally distant, physically similar, night stations.

TABLE 1 (*Continued*)

STN. PAIR	NOON STN.	NIGHT STN.	NOON CHLOR.	NOON ZOOP.	NIGHT ZOOP.	G.M. ZOOP.	NIGHT MICRO.	NOON COP.	NIGHT COP.	G.M. COP.	NOTES
C. STEP–1 Expedition, 15 September–14 December, 1960											7, 12
1	1	1	12		150		3.2				1
2	3	3	18		170		8.0				1
3	4	4	11		150		10.8				1
4	8	9	15		120		11.1				
5	10	11	8.8		80		6.6				
6	16	17	3.0		20		2.3				
7	19A	19	12		60		4.4				
8	25	23	16		80		7.4				
9	28	27	34		200		1.4				
10	34A	35	5.7		50		0.6				
11	37	38	3.0		50		1.2				
12	54A	55	9.2		140		2.0				
13	58	59	7.7		40		2.7				
14	63A	64	2.4		40		1.4				
15	68A	69	2.8		10		1.6				
16	72A	73	5.0		30		4.8				
17	76A	77	4.2		50		6.1				
18	86A	85	1.8		80		5.7				
D. TO–59–1 Expedition, 15 January–25 February, 1959											12
1	2	1	24	24	47	34	12.9				5, 8
2	4	3	18	9	18	13	0.0				9
3	6	5	41	18	10	13	0.0				10
4	8	7	22	37	88	57	12.1				
5	10	9	33	111	95	103	6.6				
6	12	11	29	98	43	65	8.1				
7	23	22	21	197	396	279	6.6				
8	29	28	24	166	239	199	11.9				
9	35	36	105	196	175	185	12.1				
10	42	41	25	91	71	80	5.5				
11	44	43	30	158	77	110	9.7				
12	46	46	107	164	130	146	5.9				1
13	47	48	36	60	121	85	6.2				
14	49	50	31	54	33	42	1.4				5
E. TO–59–2 Expedition, 13 August–22 September, 1959											11, 12
1	5	2	6.6				4.3				
2	10	8	7.5				4.6				
3	16	13	16				1.4				
4	24	21	12				3.2				
5	30	32	23				31.4				
6	34	38	9.7				8.0				
7	39	42	7.6				5.1				
8	49	52	6.8				6.1				
9	55	58	12				12.7				
10	61	64	4.4				0.5				
11	73	74	11				8.0				
12	76	79	12				9.6				
13	81	82	10				8.0				

7. Chlorophyll *a* values are for a water column 0–55 m; noon zooplankton hauls were not routinely taken.
8. Noon zooplankton was estimated; see note 5.
9. No zooplankton haul was made at station 3; the value listed is an estimate (see note 5) based on the value for an adjacent station occupied on the same night on another cruise (CalCOFI cruise 5901, station 133.60).
10. No zooplankton haul was made at station 5; the value listed was obtained as in note 9, based on station 137.40 of CalCOFI cruise 5901.
11. No zooplankton data are listed because depth of haul was very variable.
12. No copepod data available.

Chlorophyll a

The standing crop of chlorophyll *a* was estimated in mg under 1 m^2 of sea surface for a water column 100 m deep, except for Step-I where 55 m was used. This was done by taking water samples of 3–6 liters at six to eight depths in Van Dorn closing plastic samplers; filtering, extracting from the residue, and determining chlorophyll *a* concentration in the extract by optical density measurements for each sample (Richards with Thompson, 1952); using the sample data to draw a smooth profile of chlorophyll *a* with depth, and integrating the profile with a planimeter (Holmes and Blackburn, 1960). This standing crop was considered to represent, somewhat imperfectly, the standing crop of plant material (living or dead) on which animals could feed.

Some of the chlorophyll *a* data in Tables 1 and 2 have been published previously (Holmes et al., 1957; Holmes et al., 1958; Holmes and Blackburn, 1960; Blackburn et al., 1962; Scripps Institution of Oceanography, 1960, 1961). Other observations, including revisions of some values listed by Holmes and Blackburn (1960), are from R. W. Holmes (unpublished) and Griffiths (MS).

Zooplankton

Zooplankton was collected by making an oblique haul with an open subconical net between the desired maximum depth and the sea surface. The net was of the type that has been used for the past 15 years in the eastern and central Pacific by the Scripps Institution of Oceanography, U. S. Bureau of Commercial Fisheries (La Jolla and Honolulu), and Inter-American Tropical Tuna Commission (King and Demond, 1953); the mouth diameter is 1 m, the total length is about 5 m, and the mesh apertures are 0.65 mm wide in the front and middle sections and 0.31 mm in the rear section. The volume of water strained was estimated from readings of a calibrated flowmeter in the mouth of the net.

In making a haul, the ship steamed slowly to

TABLE 2

MEASUREMENTS OF STANDING CROPS OF CHLOROPHYLL *a* (mg/m^2) AND ZOOPLANKTON ($ml/10^3m^3$) AT OCEANOGRAPHIC STATIONS (stns.) IN THE EASTERN TROPICAL PACIFIC*

EXPEDITION	STN.	CHLOR.	ZOOP.	EXPEDITION	STN.	CHLOR.	ZOOP.
EASTROPIC,	33	24	193	SCOPE,	1	24	49
November	35	22	164	November–	2	25	37
1955[1]	37	25	143	December	3	43	32
				1956[2]	4	44	54
					5	51	85
					6	74	314
COSTA RICA	7	20	84		8	60	125
DOME,	12	22	250		9	24	95
November–	18	8.8	120		9C	27	250
December	22	9.6	43		9D	36	135
1959	26	12	100		10	45	166
	33	10	190		11	70	104
	36	9.4	140		16	32	95
	43	20	70		17	33	139
	46	8.7	120		18	32	114
	50–7	11	54		19	27	96
	50–16	14	56		22	59	233
	56	12	59		23	30	33
					24	33	77
					25B	49	47

* In water columns or layers to about 100 m and 300 m respectively; abbreviated as chlor. and zoop. respectively. For further explanation see text and footnotes.

[1] *Spencer F. Baird* stations; station 57 was omitted, being south of Equator and remote from others in this list; chlorophyll *a* data were extrapolated to 100 m for stations 33 and 37.

[2] Zooplankton value for station 25A was used for the adjacent station 25B.

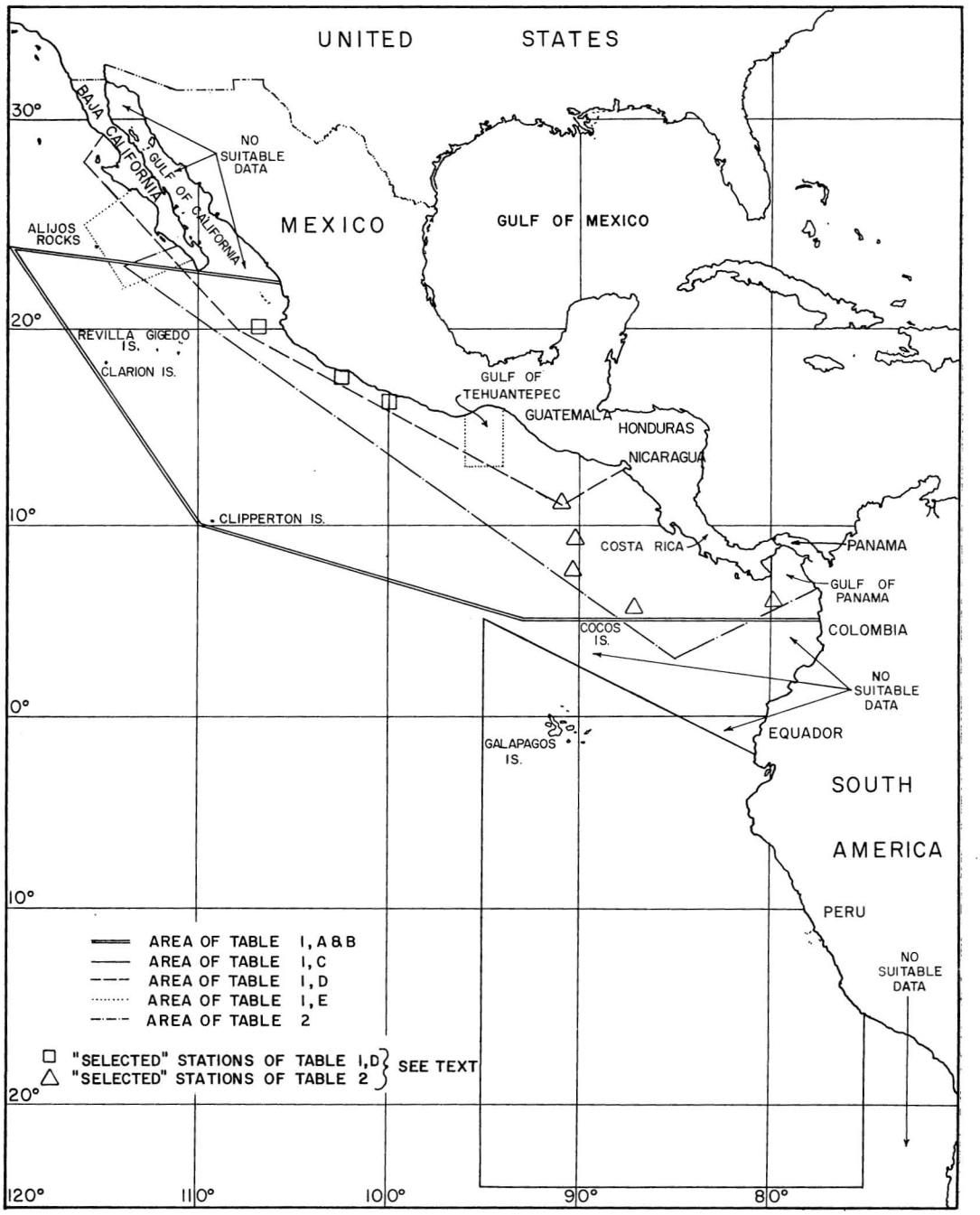

FIG. 1. Areas of groups of station-pairs and stations listed in Tables 1 and 2, and positions of "selected" stations from some groups. (See Fig. 2 for all station-pairs of Table 1, A and B.)

try to maintain a wire angle of 45°. Generally a maximum depth of 300 m was desired, but actual depths range from 203 to 401 m for hauls listed in Tables 1 and 2. At some stations identified in Table 1, the hauls were made to a desired maximum depth of 140 m (actual depths from 126 to 145 m); in each of these cases the zooplankton volume for a haul to 300 m was estimated as explained in Appendix I from the volume obtained, and the estimate (only) was listed and used in the analysis.

Measurement of standing crop was expressed as milliliters of displacement volume of the catch of small organisms (i.e., excluding organisms >5 cm in length or >5 ml in volume) per 10^3m^3 of water strained. This was regarded as a very imperfect estimate of standing crop of herbivores, because the net catches many primary carnivores but not all herbivores. An attempt to minimize these difficulties for some of the zooplankton data is described below (see section on Copepods).

Most of the zooplankton measurements in Tables 1 and 2 have been published previously (see references in section on Chlorophyll *a*, above); other observations, namely those for Table 1, B, are from Griffiths (MS).

Micronekton

Micronekton, which consists of active animals about 1 to 10 cm long, was collected with the large net and towing routine described by Blackburn and associates (1962:31–32). In brief, an oblique haul was made between 90 m (on the average; actual depths ranged from 72 to 115 m) and the sea surface, from a ship steaming at about 5 knots, with a large open subpyramidal net of uniform mesh aperture about 5.5 mm by 2.5 mm. Watery planktonic organisms were discarded from the catch, which was then sorted into its fish, cephalopod, and crustacean components; displacement volumes of these components were measured. The volume of water strained was estimated from the mouth-area of the net (2.3 m^2), the distance steamed during the haul, and a filtration coefficient of 0.757. The coefficient was measured in the way described by Blackburn and associates (1962); a subsequent experiment yielded a similar value, 0.738.

Measurements of standing crop were expressed in $ml/10^3m^3$ of water strained. For the purpose of this study only the fish and cephalopod components (combined) are considered. These may be regarded, in the main, as primary carnivores, but the crustacea are probably a mixture of herbivores, primary carnivores, detritus feeders, and omnivores; it is probable that some fish and cephalopods avoid the net. The author is responsible for these data in Table 1, none of which have been published previously in their present form.

Copepods

Measurements of standing crop of copepods from the zooplankton are available for two cruises, for which it was thought to be particularly important to have a better measurement of herbivore standing crop than that given by zooplankton. Even this measurement is imperfect, because some herbivores are excluded and some copepods are probably carnivorous. The data are from R. C. Griffiths (unpublished). They were obtained by a volumetric method, which is essentially that of Yentsch and Hebard (1957) with minor refinements (Griffiths and Fee, MS), and are expressed in $ml/10^3m^3$ of water strained. The manual sorting of copepods from the zooplankton is so time-consuming that no attempt was made to provide similar data for all cruises.

The copepod volumes are all much lower than the corresponding volumes of zooplankton (Table 1, A and B); they average 4.3% of the zooplankton and none is higher than 12%, although a figure of a much higher order was indicated by gross inspection of most of the unsorted zooplankton samples. This is clearly an effect of the different volumetric method which was used for the copepods; interstitial water is far more efficiently removed by this method than by the ordinary filtration method which was employed for the unsorted zooplankton. Possibly it is also an effect, due to shrinkage in formalin, of the later date at which the copepod measurements were made.

The volumes of zooplankton and carnivorous micronekton may not be precisely comparable either, although both were measured by the same (ordinary filtration) method at about the same

time: the former, being more heterogeneous and consisting of smaller animals (many of which have numerous appendages), probably retains more interstitial water after filtration than does the latter. Therefore these three sets of measurements lack the common biological base that the common unit, $ml/10^3m^3$, might suggest.

Stations

The standing crop of chlorophyll *a* was routinely measured at stations occupied about local noon, so that it might be compared (for other purposes) with measurements of primary production and submarine daylight; the latter are most conveniently made or started about noon. There was seldom enough time to take water samples for chlorophyll *a* at night stations, and when this was done the number of sampled depths was generally only four. On the other hand, the crop of micronekton was generally measured at stations occupied about local midnight, because of diurnal vertical migration (King and Iversen, 1962); it would have been necessary to lower the net to a much greater depth to obtain similar samples in the daytime, and time did not permit this. These and other research requirements of the cruises dictated a schedule of two major stations per day, at about local noon and midnight, on the cruises listed in Table 1. Generally a zooplankton haul was made at each of these stations except on Step-I, where it was frequently omitted at the noon station.

As a result there are no stations at which acceptable measurements of all three standing crops were made at the same time and place, although a few such sets of measurements were obtained within <36 hr at the same place (Table 1, footnote 1). For this study it was decided to pair adjacent noon and night stations which were separated by <120 miles (see numbered lines of varying length, e.g., *B1* in Fig. 2) and <36 hr. Within these limits, the stations to be paired were chosen to (a) maximize the number of station-pairs, and (b) minimize differences in time, space, and physico-chemical conditions within pairs. Five pairs were discarded because the ratio, night zooplankton/noon zooplankton, exceeded the highest such ratio observed at the same place (i.e., 2.4 for pair A4 in Table 1); it was thought that such high ratios might signify large differences in biological conditions between adjacent stations.

The remaining 81 pairs are listed in Table 1. Zooplankton data are not given for TO–59–2 because haul depth was very variable (the ship could not maintain the desired speed). For each station-pair on the other four cruises, there are available for analysis one measurement of standing crop of chlorophyll *a*, one of zooplankton, and one of carnivorous micronekton. The zooplankton value is the geometric mean of the listed noon and night values, except for Step-I, where it is the night value.

Measurements of copepod standing crops are given for each noon and night station in Table 1, parts A and B, in the same way as the crops of zooplankton of which they formed part. The value used for each station-pair in the statistical analysis was the geometric mean of noon and night values, corresponding to the similar statistic for zooplankton. The coefficient of correlation between the two sets of geometric means is +0.881, which is significant at the 1% level of probability.

Table 2 shows only pairs of chlorophyll *a* and zooplankton measurements. Each pair refers to a single station which was occupied generally about local noon.

Positions of station-pairs and stations listed in Tables 1 and 2 may be found as follows: Table 1, A—Holmes and Blackburn (1960), also Figure 2 of this paper; Table 1, B—Griffiths (MS), also Figure 2 of this paper, also Blackburn and associates (1962, Fig. 2); Table 1, C—Scripps Institution of Oceanography (1961); Table 1, D and E—Blackburn et al. (1962); Table 2—Holmes et al. (1957) for Eastropic, Holmes et al. (1958) for Scope, and Scripps Institution of Oceanography (1960) for Costa Rica Dome.

STATISTICAL ANALYSIS: RELATIONS BETWEEN VARIABLES

General

Table 3 gives total and partial correlation coefficients among standing crops for the station-pairs of Table 1 and stations of Table 2. Parts A and B of Table 1, representing two cruises made in the Northern Hemisphere spring, have

been combined for this and all subsequent parts of the analysis. The different parts of Table 2, representing three cruises made in the Northern Hemisphere autumn, have been similarly combined. All statistics were calculated with the logarithms of the measurements; micronekton data in Table 1D were first raised by 0.1 to eliminate zeros.

The two-variable regressions given below are structural regressions fitted, estimated, and investigated by the methods of Bartlett (1949). These methods are appropriate when each variable is subject to error and when the functional relationship, rather than a predictive one, is of interest. They include the estimation of confidence limits and tests of linearity. In these regressions C, Z, M, and H are logarithms of standing crops of chlorophyll *a,* zooplankton, carnivorous micronekton, and copepods, respectively. The grouping of points for Bartlett's method was done on the basis of C values for each regression except (6), where it was done on the basis of Z values. The assumption of a linear relationship among points was validated at the 5% level of probability in each regression except (8); in (8) departure from linearity was significant at the 5% level but not at the 2.5% level.

According to Bartlett (1949), the joint confidence region for the parameters of slope and position of the above-mentioned type of regression, i.e., the region in which the true relationship is likely to lie, is elliptical. For the regressions of this paper for which such regions were of interest, it was found that the sides of the ellipses were nearly straight over most of the range of the observations, and they were accordingly drawn as straight lines in Figures 3, 4, and 5.

The positions of the regressions are of little biological interest or significance, except in a few instances mentioned in the discussion, for such reasons as: differences in amount of interstitial water included in Z, M, and H; the omission of some material of the trophic level that it was desired to measure, and/or the inclusion of some material of another trophic level, in Z, M, and H; and differences in the ways in which some crops were measured on certain cruises, namely C with respect to depth in Table 1, C, and Z with respect to time of day in Table 1, C and in Table 2. However, the slopes of the regressions may be considered significant biologically, because the measurements of a given crop for a given cruise are probably all comparable, methodologically.

Chlorophyll a, *Zooplankton, and Carnivorous Micronekton*

The largest set of data (n = 36) is for the combined two cruises of the Northern Hemisphere spring (Table 1, A and B). This set is henceforth called AB–36–Z. Figure 2 shows where the observations were made.

TABLE 3

TOTAL AND PARTIAL CORRELATION COEFFICIENTS AMONG LOGGED STANDING CROP DATA FOR STATION-PAIRS IN TABLE 1 AND STATIONS IN TABLE 2†

SOURCE OF DATA	n	r_{cz}	r_{cm}	r_{zm}	$r_{cz.m}$	$r_{cm.z}$	$r_{zm.c}$	
Table 1, A and B	36	+0.702**	+0.615**	+0.626**	+0.515**	+0.345*	+0.317	[1]
Ditto, selected data	11	+0.966**	+0.860**	+0.840**	+0.880**	+0.348	+0.068	[2]
Table 1, C	18	+0.718**	+0.314	+0.365	+0.682**	+0.078	+0.207	
Table 1, D	14	+0.376	+0.137	+0.781**	+0.435	−0.271	+0.794**	
Table 1, E	13		+0.592*					
Table 2	35	+0.124						
		r_{ch}	r_{cm}	r_{hm}	$r_{ch.m}$	$r_{cm.h}$	$r_{hm.c}$	
Table 1, A and B	36	+0.613**	+0.615**	+0.602**	+0.386*	+0.390*	+0.361*	[3]
Ditto, selected data	8	+0.929**	+0.874**	+0.849**	+0.728	+0.440	+0.202	[4]

[1] Series AB–36–Z [2] Series AB–11–Z [3] Series AB–36–H [4] Series AB–8–H

† The letters c, z, h, and m indicate chlorophyll *a,* zooplankton, copepods, and carnivorous micronekton respectively, * and ** indicate significance at 5 and 1 % levels of probability, and n is number of station-pairs or stations; see text for particulars of "selected data."

The correlation coefficients of Table 3 show that Z and M are independently related to C, and related to each other through their common association with C, but not otherwise. The regressions on C are

$$Z = 1.8306 + 0.634\ (C - 1.2647) = 1.0288 + 0.634\ C \ldots (1)$$

$$M = 0.7787 + 0.668\ (C - 1.2647) = -0.0661 + 0.668\ C \ldots (2)$$

where 1.2647, 1.8306, and 0.7787 are means of C, Z, and M; the corresponding antilogarithms are 18.40 mg/m^2 of chlorophyll *a*, 67.70 ml/10^3m^3 of zooplankton, and 6.01 ml/10^3m^3 of carnivorous micronekton. The 95% confidence limits of the regression (slope) coefficients in (1) and (2) are 0.639 ± 0.211 (0.428 to 0.850) and 0.663 ± 0.302 (0.361 to 0.965). The differences between such figures as 0.634 and 0.639, 0.668 and 0.663, etc., in this paper arise from features of the regression methods used by Bartlett (1949). The fitted regressions and 95% confidence limits for the regression relationships are shown in Figures 3 and 4 as solid lines and dashed lines.

Points within the confidence limits indicate the station-pairs at which the relationship between C and Z (Fig. 3), or C and M (Fig. 4), is closest to the real relationship which exists between the variables for all station-pairs. Figures 3 and 4 show several points within the confidence regions, but only three of the station-pairs represented by these points are common to both regions. For analytical purposes it was thought permissible to consider additional station-pairs, which were represented by points

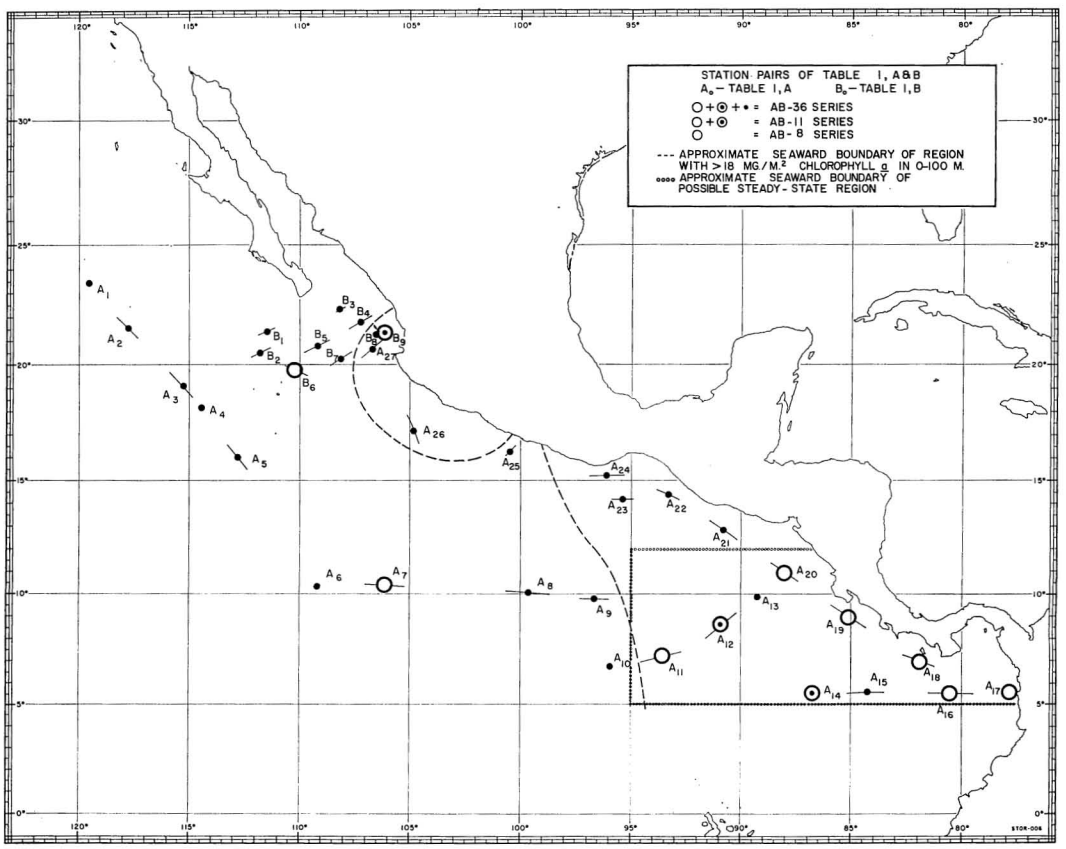

FIG. 2. Station-pairs of Table 1, A and B (Northern Hemisphere Spring), showing the series AB–36, AB–11, and AB–8, discussed in text; approximate boundaries of high-chlorophyll and steady-state regions shown.

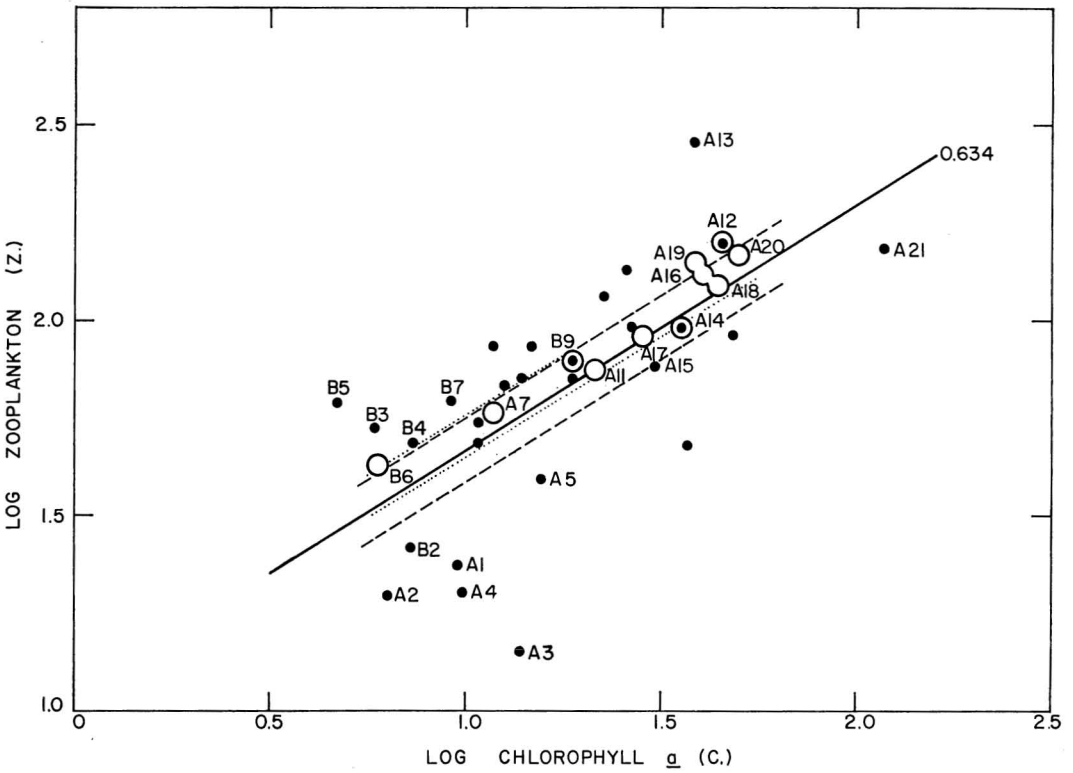

FIG. 3. Relationship between logarithm chlorophyll *a* (C) and logarithm zooplankton (Z) for the 36 station-pairs of Table 1, A and B (AB–36 series). Antilogarithms are in mg/m^3 over 0–100 m and ml/10^{3}m^3 over 0–300 m. Station-pairs in series AB–11 and AB–8 are identified as in Fig. 2. The solid line (——) is the fitted structural regression of Z on C and the dashed lines (----) are the 95% confidence limits of the regression, both for the AB–36 series; the dotted lines (.....) are the 95% confidence limits of a similar regression for the AB–11 series.

falling within the 95% confidence region for either of the regressions and just outside this region for the other regression. There were 8 of these, making 11 station-pairs for which the observed Z and M were both related to C in a way close to the real relationships. The set of data from these pairs is henceforth called AB–11–Z. The localities are shown by circles (with or without enclosed dots) in Figures 2, 3, and 4.

Correlation coefficients for these 11 station-pairs show that Z and M are related to C, Z independently of M, but M not independently of Z; and related to each other through their common association with C, but not otherwise (Table 3, "selected data"). The regressions on C for the 11 pairs, corresponding to (1) and (2) for 36 pairs, are

$$Z = 1.9707 + 0.619\ (C - 1.4287) = 1.0863 + 0.619\ C \ldots (3)$$

$$M = 0.8665 + 0.666\ (C - 1.4287) = -0.0850 + 0.666\ C \ldots (4)$$

with 95% confidence limits of the regression coefficients respectively 0.658 ± 0.152 (0.506 to 0.810) and 0.773 ± 0.522 (0.251 to 1.295). The 95% confidence limits for the regression relationships are shown as dotted lines in Figures 3 and 4.

The similarity of the two regression coefficients for AB–36–Z, and likewise for AB–11–Z, suggest a coefficient near 1.0 for the regression of M on Z. Such values (1.054 for AB–36–Z, 1.077 for AB–11–Z) are obtained when points are grouped for Bartlett's method in the same

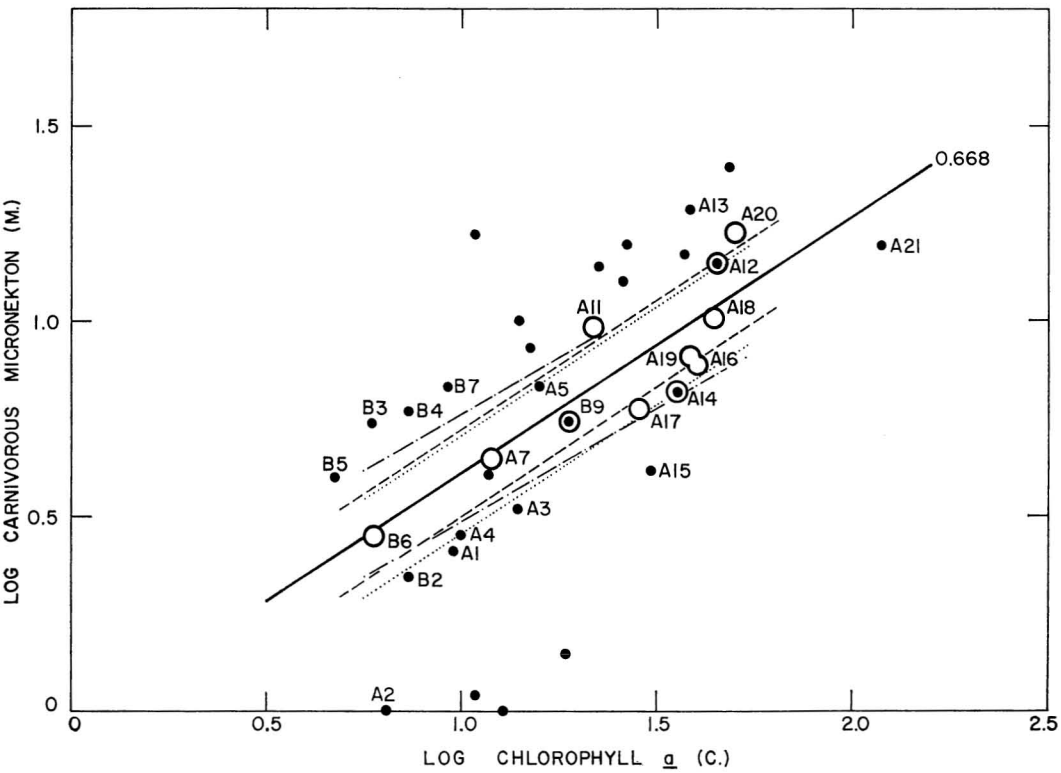

FIG. 4. Relationship between logarithm chlorophyll *a* (C) and logarithm carnivorous micronekton (M) for the 36 station-pairs of Table 1, A and B (AB–36 series). Antilogarithms are in mg/m² over 0–100 m and ml/10³m³ over 0–90 m. Station-pairs in series AB–11 and AB–8 are identified as in Fig. 2. The solid line (——) is the fitted structural regression of M on C and the dashed lines (----) are the 95% confidence limits of the regression, both for the AB–36 series; the dotted lines (.....) and dashed-and-dotted lines (-.-.-.-) are the 95% confidence limits of similar regressions for the AB–11 and AB–8 series.

way as for the equations above, i.e., on the basis of C values. If points are grouped on the basis of Z values the corresponding coefficients are 0.799 and 0.952.

For the less numerous data of the Southern Hemisphere spring (Table 1, C), only the regression of Z on C is significant (Table 3). It is

$$Z = 1.8153 + 0.702\ (C - 0.8457) = 1.2195 + 0.702\ C \ldots (5)$$

where 0.8457 and 1.8153 are means of C and Z, with antilogarithms 7.06 mg/m² of chlorophyll *a* and 65.39 ml/10³m³ of zooplankton; the antilogarithm of mean M for this series of station-pairs is 3.37 ml/10³m³. Mean C is much lower than in AB–36–Z, reflecting the shorter water column over which it was measured. The 95% confidence limits of the regression coefficient are 0.701 ± 0.359 (0.342 to 1.060).

For the still less numerous data of the Northern Hemisphere winter (Table 1, D), neither Z nor M have a significant regression on C (Table 3). This may reflect the small n (=14) and the narrow range of C; the latter is 1.3222–2.0294, which may be compared with 0.2553–1.5315 for 18 differently-measured observations in Table 1, C and 0.6812–2.0792 for 36 similarly-measured observations in Table 1, A and B. The difference in range of C may be explained by the fact that the data of Table 1, D are all from inshore localities (Fig. 1); the other two series are from both inshore and offshore locations (Fig. 1), where C values tend to be high and low respectively (Fig. 2).

Since these data were obtained in exactly the same way as those in Table 1, A and B, their logarithms may be inspected to see if any of them fall within the confidence regions of regressions (3) and (4) in Figures 3 and 4. These confidence regions are considered to be more interesting than those of regressions (1) and (2), for reasons given later. The data of 3 station-pairs (numbers 5, 10, and 11 in Table 1, D; shown as "selected stations" in Fig. 1) fall within these regions, in the same way as the 11 station-pairs of the Northern Hemisphere spring.

The significant relation between Z and M (Table 3) is

$$M = 0.6018 + 1.075\ (Z - 1.8586) = -1.3962 + 1.075\ Z \ldots (6)$$

where 1.8586 and 0.6018 are means of Z and M, with antilogarithms 72.21 ml/10^3m^3 of zooplankton and 4.00 ml/10^3m^3 of carnivorous micronekton (the last figure is 0.10 higher than the true geometric mean of micronekton values); the antilogarithm of mean C for this series of station-pairs is 32.80 mg/m^2 of chlorophyll *a*. The 95% confidence limits of the regression coefficient are 0.915 ± 0.816 (0.099 to 1.731).

The observations for the Northern Hemisphere summer (Table 1, E) are still fewer (n = 13), and for Z their quality is unacceptable; C and M are significantly related (Table 3) as

$$M = 0.7255 + 1.254\ (C - 0.9910) = -0.5172 + 1.254\ C \ldots (7)$$

where 0.9910 and 0.7255 are means of C and M, with antilogarithms 9.80 mg/m^2 of chlorophyll *a* and 5.32 ml/10^3m^3 of carnivores; the range of C is 0.6435–1.3617. The 95% confidence limits of the regression coefficient are 1.138 ± 1.589 (−0.451 to 2.727). These limits include those of the corresponding coefficients in (2) and (4), and are too wide to have much analytical importance.

It is of greater interest to see if any of the logarithm-pairs of Table 1, E fall within the confidence region of regression (4) in Figure 4. One of them does but it may be ignored: the Z data, though imperfect, showed that the corresponding point for C and Z would probably have fallen well outside the confidence region of regression (3) in Figure 3.

The data for the Northern Hemisphere autumn (Table 2) consist only of observations of C and Z. They are not significantly related (Table 3) despite a fairly high n (= 35); possible explanations may be found in the narrow range of C (0.9395–1.8692), which probably reflects the lack of observations far offshore, and the large number of stations (about 15) located in the upwelling area of the Costa Rica Dome. Antilogarithms of mean C and mean Z are 25.02 mg/m^2 of chlorophyll *a* and 97.77 ml/10^3m^3 of zooplankton.

The Z data in this series represent noon hauls, whereas those of Figure 3 represent means of noon and night hauls. It can be shown from Table 1, A and B that the former average 0.05 less than the latter for the same station-pairs. The dotted lines representing the confidence limits of regression (3) in Figure 3 were therefore lowered by 0.05 on the Z coordinate, so that the data of Table 2 could be compared with them. It was found that the data of 5 stations of Table 2 fell within these limits: namely, Costa Rica Dome stations 22, 43, and 50–16, and Scope stations 8 and 16, which are shown as "selected stations" in Figure 1.

Chlorophyll a, *Copepods, and Carnivorous Micronekton*

These three standing crops (C, H, and M) can be compared only for the combined two cruises made in the Northern Hemisphere spring (Table 1, A and B). This set of data is called AB–36–H. The correlation coefficients of Table 3 reveal a set of relationships like those between C, Z, and M, except for a significant relationship between H and M which is independent of their common association with C.

Figure 5 shows the regression of H on C, corresponding to that of Z on C in (1) and in Figure 3; it is

$$H = 0.4686 + 0.652\ (C - 1.2647) = -0.3560 + 0.652\ C \ldots (8)$$

where 0.4686 is mean H, with antilogarithm 2.94 ml/10^3m^3 of copepods. The 95% confidence limits of the regression coefficient are

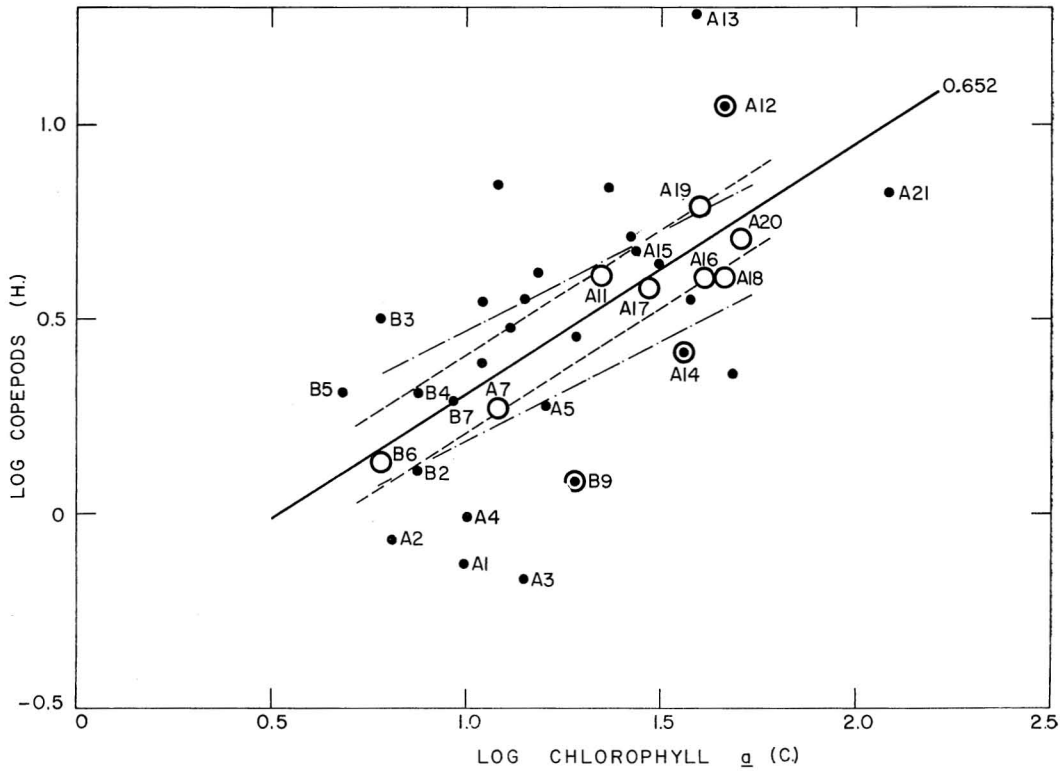

FIG. 5. Relationship between logarithm chlorophyll *a* (C) and logarithm copepods (H) for the 36 station-pairs of Table 1, A and B (AB–36 series). Antilogarithms are in mg/m^2 over 0–100 m and ml/10^{3}m^3 over 0–300 m. Station-pairs in series AB–11 and AB–8 are identified as in Fig. 2. The solid line (——) is the fitted structural regression of H on C and the dashed lines (----) are the 95% confidence limits of the regression, both for the AB–36 series; the dotted-and-dashed lines (-.-.-.-) are the 95% confidence limits of a similar regression for the AB–8 series.

0.657 ± 0.263 (0.394 to 0.920). The fitted regression is shown in Figure 5 as a solid line and the 95% confidence limits of the relationship as dashed lines.

Points within the confidence regions of regressions (8) and (2) were compared, as described above; 8 station-pairs, for which the observed H and M were both related to C in a way close to the real relationships, were identified. They were included in the 11 station-pairs for which similar statements were made about Z, M, and C, and are identified by plain circles in Figures 2, 3, 4, and 5; the other 3 station-pairs are identified by circles with enclosed dots. This set of data, i.e., of C, H, and M from the 8 station-pairs, is henceforth called AB–8–H.

Correlation coefficients in AB–8–H (Table 3) include no significant partial coefficients, although $r_{ch.m}$ is very close to significance at the 5% level of probability; all total coefficients are highly significant. The regressions on C for AB–8–H, corresponding to (8) and (2) for AB–36–H, are

$$H = 0.5308 + 0.517\ (C - 1.4023) = -0.1942 + 0.517\ C \ldots (9)$$

$$M = 0.8543 + 0.583\ (C - 1.4023) = 0.0368 + 0.583\ C \ldots (10)$$

with 95% confidence limits of the regression coefficients respectively 0.250 ± 0.494 (−0.244 to 0.744) and 0.558 ± 0.517 (0.041 to 1.075). The 95% confidence limits for the regression relationships are shown as dashed-and-dotted lines in Figures 4 and 5.

The similarity of the two regression coefficients for AB–36–H, and likewise for AB–8–H, suggest a coefficient near 1.0 for the regression of M on H. Such values (1.025 for AB–36–H, 1.128 for AB–8–H) are obtained when points are grouped for Bartlett's method on the basis of C values. If points are grouped on the basis of H values the corresponding coefficients are 0.701 and 1.091.

DISCUSSION

Recognition of Possible Steady-state Situations

A steady state among standing crops of phytoplankton, herbivores, and primary carnivores could be defined as a state in which material added to each trophic level (by photosynthesis, or by feeding on the level below) is continuously balanced by material lost from it (some assimilated by the level above, and some lost by other kinds of death, respiration, sinking, and active or passive emigration).

Measurements of the three standing crops in a number of different situations could be considered consistent with the steady-state hypothesis if: (i) all total correlation coefficients were positive and significant, (ii) the partial correlation coefficient of phytoplankton and herbivores was positive and significant, and (iii) the other two partial correlation coefficients were nonsignificant. In explanation of (iii), a significant positive partial correlation between phytoplankton and carnivores, independent of herbivores, would not be biologically realistic under the steady-state hypothesis; and a similar coefficient between herbivores and carnivores, independent of phytoplankton, could signify some geographical redistribution of biota at the higher trophic levels (e.g., carnivores moving from herbivore-poor to herbivore-rich areas), and probable violation of the hypothesis.

Table 3 shows that conditions (i), (ii), and (iii) are fulfilled only for the AB–11–Z set of observations, considering all zooplankton as herbivores. Conditions (i) and (iii) are fulfilled and condition (ii) is almost fulfilled for the AB–8–H set in which copepods only were considered as herbivores; in this case the partial correlation coefficient of phytoplankton and herbivores is positive and nearly significant with only 5 degrees of freedom.

The group of 11 or 8 station-pairs represents a statistical, objective selection of a smaller set of pairs from a larger set. The data of the larger set of pairs satisfied conditions (i) and (ii) but not (iii), and it was thought that the data of the smaller set might satisfy all three conditions.

If a steady state exists, the standing crop of chlorophyll *a* might be expected to be positively correlated with primary productivity (production rate) in the same water column. This cannot be shown for the smaller group of station-pairs because productivity was estimated at only 6 of the 11 noon stations, and the incubation method and depth of sampled column were not the same for all 6. It can be shown for the 19 noon stations of Table 1, A, for which comparable water-column (0–100 m) productivity data are available (see Table 4, unpublished data from R. W. Holmes). The measurements were made by the C_{14} method using a constant-illumination "laboratory" incubator (Blackburn et al., 1962);

TABLE 4

PRODUCTIVITY (PRIMARY PRODUCTION RATE) FOR WATER COLUMN 0–100 M AT NOON STATIONS LISTED IN TABLE 1, A*

STN.	PROD.	STN.	PROD.	STN.	PROD.	STN.	PROD.
6	5.2	32	5.0	62	31.0	86	3.2
8	7.1	34	9.5	72	8.0	100	14.8
13	3.2	49	28.3	74	5.0	122	23.4
15	1.8	56	11.0	76	74.0	139**	15.0
23	11.5	58	11.8	79	10.8		

* In $mgC/m^2/hr.$; obtained by the C_{14} method, samples incubated at 1,000 foot-candles; unpublished values from R. W. Holmes, based on sample data listed by Blackburn et al., 1962, Appendix I.

** Productivity data for this station were listed for station 137 in Blackburn et al., 1962, Appendix I.

the correlation coefficient of logarithms of chlorophyll *a* and productivity is +0.532, significant at the 5% level. Estimates of water-column productivity for noon stations of Table 1, B were made using a simulated *in situ* "deck" incubator (Blackburn et al., 1962), and to a depth of only 40 m; they are not significantly correlated with chlorophyll *a* at 0–100 m ($r = +0.461$) but the data (not given here) are available for only 8 stations. It may be said that the available productivity data do not deny the existence of steady-state conditions for the station-pairs of the smaller group—at least for those listed in Table 1, A, which are all located south of 12°N.

Figure 2 shows that 8 of the 11 and 6 of the 8 station-pairs occur in the region bounded by 12°N, 95°W, 5°N, and the American coast. In this region there are only 2 station-pairs, A13 and A15, for which the standing crop data do not agree closely with the regressions describing at least one of the above-mentioned sets of data (AB–11–Z or AB–8–H). The data for A15 do not deviate much from the regressions (Figs. 3, 4, and 5). Those for A13 deviate considerably; this is not surprising because A13 is in an upwelling area, the Costa Rica Dome (Wyrtki, 1964), where a steady state would not be expected.

It is clear that station-pairs fulfilling steady-state conditions were largely confined to and characteristic of a particular ocean area, in the northern spring of 1958. It is more likely that ocean conditions permitting the existence of a steady state would be distributed in this way, than that they would occur in a number of scattered areas. This is discussed below.

It is of interest to classify the other station-pairs for which the data deviate from the regressions. For this purpose the C, Z, and M observations were used, and a station-pair was considered deviant if it fell clearly outside the confidence region of either regression (3) or (4), i.e., outside dotted lines in Figure 3 or 4. The deviations were classified as to whether Z and M values were above, within, or below the confidence limits of the regression on C. The classification of the 36 pairs of Table 1, A and B, including the 11 nondeviant ones, is in Table 5.

Table 5 shows that all but one of the possible combinations of values of Z and M (compared with C) were encountered. The most common combination was the one discussed above, with both Z and M in confidence limits (AB–11–Z); the two next most frequent combinations were those with Z and M both high, and both low, compared with C; other combinations occurred much less frequently. The station-pairs are all identified in Figure 2.

Table 5 also shows that 9 of the 11 station-pairs consistent with steady-state conditions are

TABLE 5

CLASSIFICATION OF STATION-PAIRS OF TABLE 1, A AND B (SERIES AB–36), ACCORDING TO WHETHER Z AND M VALUES FALL ABOVE, WITHIN, OR BELOW THE CONFIDENCE LIMITS OF THEIR REGRESSIONS, (3) AND (4), ON C*

Z	M	PAIRS WITH C> MEAN	PAIRS WITH C< MEAN	NO. PAIRS
Within	Within	[A11–12, A14, A16–A20] B9	A7, B6	11
Above	Above	A13, A24, A26	A8 [B3–5, B7]	8
Below	Below	A15, A21	[A1–4, B2]	7
Within	Above	A23	A10, A25	3
Within	Below	B8	A6, B1	3
Above	Within		A9	1
Below	Within		A5	1
Above	Below			0
Below	Above	A22, A27		2
TOTAL		18	18	36

* Station-pairs with C values above and below the mean are distinguished. Groups of geographically adjacent station-pairs within each class are bracketed.

in the region of higher-than-average chlorophyll *a* (Fig. 2) and account for half the pairs in this region; whereas, of the other 25 station-pairs, 16 are in the region of lower-than-average chlorophyll *a* and account for nearly all the station-pairs in that region. This is interesting because the high-chlorophyll area along the central American coast is a fairly eutrophic area; it is comparable in surface chlorophyll *a* and surface productivity with the region off southern California (Holmes, 1958). It has been supposed that steady-state conditions occur (a) in oligotrophic tropical ocean areas, but (b) not in eutrophic tropical ocean areas (Cushing, 1959*b*). The data of this paper oppose (b), and this point is further discussed below. They cannot confidently be said to oppose (a) because other relationships consistent with steady-state conditions, besides those represented by the regressions in Figures 3 and 4, could exist for certain groups of station-pairs. In this connection, Table 5 shows that 4 adjacent pairs (B3, 4, 5 and 7, all at the mouth of the Gulf of California; see Fig. 2) have high values of Z and M, whereas 5 other adjacent pairs farther west (A1–4 and B2) have low values of Z and M. Figures 3 and 4 show that the range of C is about the same for both groups. The difference between these groups might be an effect of year (the A data are from 1958, the B data from 1960) rather than of area. The matter warrants further attention when more data are available.

Station-pair A4 was off Clarion Island. This area was visited on another cruise (Island Current Survey) in May 1957, and the oceanographic data then obtained were presented by Bennett and Schaefer (1960). Chlorophyll *a* in a water column 0–80 m averaged 18.0 mg/m^2 for 10 offshore stations, and zooplankton (in hauls made like those described in this paper, at various times of day) averaged 16 ml/10^{3}m^3 for 10 offshore stations. The point corresponding to these measurements would fall well below the confidence region, and not far from A1–4, in Figure 3.

The productivity data of Table 4 are not obviously helpful in explaining the different kinds of deviations from regression shown in Table 5. For instance, a structural regression, fitted to the data of Table 4 and the corresponding chlorophyll *a* data from Table 1, A, showed that the most deviant noon stations were 15 and 76, corresponding to station-pairs A5 and A21; their productivities were respectively very low and very high for the chlorophyll *a*, but they do not help to interpret the particular combinations of C, Z, and M observed.

Biological Significance of Regression Statistics

As mentioned above, the regression (slope) coefficients are likely to have biological significance. Those involving Z or H on C are of special interest because of the many previous studies of relationships between phytoplankton and zooplankton crops. In regression (3), of Z on C, for the AB–11–Z set of station-pairs with all standing crops consistent with steady-state conditions, the point estimate of the coefficient is 0.619 with 95% confidence limits 0.506 to 0.810. In (9), H on C, for the AB–8–H set with data less certainly consistent with steady-state conditions, the corresponding figures are 0.517 and –0.244 to 0.744. Similar point estimates and confidence limits are available for three other significant regressions of Z or H on C (equations (1), (5), and (8)) in which steady-state conditions could not be demonstrated; they are respectively 0.634 (0.428 to 0.850), 0.702 (0.342 to 1.060), and 0.652 (0.394 to 0.920). Equation (1), reworked for the 27 station-pairs of Table 1, A which were all occupied in 1958, gave a point estimate 0.829 and limits 0.508 to 1.150. It may be concluded that the standing crop of herbivores generally varies with some power less than 1.0 of the standing crop of phytoplankton when there is a significant relationship between them, whether or not steady-state conditions prevail among all standing crops. This implies that herbivores utilize phytoplankton with increasing inefficiency as standing crop of the latter increases, which is consistent with the observations of some workers (Cushing, 1959*a*, *b*; Beklemishev, 1962; and references cited there) on excessive feeding by herbivorous copepods: when phytoplankton is abundant the herbivores may kill more of it than they assimilate.

In significant regressions of M on Z or H the coefficients are evidently much closer to 1.0 than

those for Z or H on C, as noted above, whether or not steady-state conditions prevail. For the material of Table 1, D (equation [6]), where $r_{zm.c}$ is significant, the point estimate is 1.075 with 95% confidence limits 0.099 to 1.731. For the material of Table 1, A and B, the following eight point estimates are available from various regressions noted above: 0.701, 0.799, 0.952, 1.025, 1.054, 1.077, 1.091, and 1.128. They differed in *n*, in the independent variable (Z or H), in the basis of point-grouping for Bartlett's line-fitting method, and in the significance of the partial correlation coefficient. It may be concluded that the standing crop of primary carnivores generally varies in an approximately linear way with that of herbivores, when there is a significant relationship between them, whether or not steady-state conditions exist among all standing crops. This means that primary carnivores utilize herbivores with about the same efficiency at different levels of herbivore standing crop.

The positions of the regressions are not nearly as informative as their slopes, for methodological reasons given above, but a few interesting comparisons of the means of paired variables can be made. Standing crops of chlorophyll *a* and copepods can be estimated very approximately in terms of a common unit, mgC/m^3. For AB–36–H the mean crop of chlorophyll *a* is 18.40 $mg/10^2m^3$ in the upper 100 m, and the mean of copepods (free of interstitial water) is 2.94 $ml/10^3m^3$ in the upper 300 m. The latter, converted as in Appendix I, becomes 5.00 $ml/10^3m^3$ in the upper 140 m, and it is assumed for the present purpose that the same concentration exists in the upper 100 m. The mean amounts of chlorophyll *a* and copepods per cubic meter in the upper 0–100 m are then 0.184 mg and 0.005 ml. The latter may be taken as 0.640 mg dry weight, using the ratio of 128 mg/ml given by Tranter (1960) for warm-oceanic zooplankton, predominantly copepods, free of interstitial water when measured by volume. The corresponding weights of carbon per cubic meter are estimated as 5.52 mg for the phytoplankton (multiplying weight of chlorophyll *a* by 30, after Strickland, 1960) and 0.24 mg for the copepods (considering carbon as 38% of dry weight, following Curl, 1962). The ratio, copepod C/plant C, is then 0.043; it would, of course, be much higher for total-herbivore carbon or zooplankton carbon. It is a very rough estimate. For instance, a higher factor than 30, e.g., 60, could have been used to estimate C from chlorophyll *a* (Strickland, 1960), and the concentration of copepods could be higher in the upper 100 m than in the upper 140 m (Thrailkill, 1956); either of these could affect the ratio, although both together might not change it much. For AB–8–H the same procedures give values of 7.58 and 0.28 mgC/m^3, with ratio 0.037.

The standing crops of zooplankton and carnivorous micronekton cannot be expressed realistically as carbon, because of taxonomic heterogeneity and interstitial water. They can be compared in $ml/10^3m^3$, with many reservations. Taking Z and M antilogarithms in AB–36–Z and AB–11–Z, and estimating zooplankton in the upper 140 m as before, the following ratios (carnivorous micronekton/zooplankton) are obtained: $6.0/136.0 = 0.044$, and $7.4/191.0 = 0.039$.

The two copepod/phytoplankton and two carnivore/zooplankton ratios, one of each from a set of data consistent (or almost so) with steady-state conditions and the other not, are all about 0.04. Under steady-state conditions, ratios between total standing crops at successive trophic levels will be approximately the ratios between supplies of food available to the successive levels—i.e., "food-chain efficiency ratios," which are expected to be between 0.06 and 0.15 (Slobodkin, 1960). It is therefore emphasized for the copepod/phytoplankton ratios that the numerators, if considered to represent all herbivores, are too low. Similarly for the carnivore/zooplankton ratios, the numerators, if considered to represent all primary carnivores, are too low; the denominators, if considered as herbivores, are too high; and the denominators probably include more interstitial water, proportionate to their size, than the numerators. Thus the ratios given above are probably all too low, if considered as ratios between total crops at successive trophic levels, and need not be considered deviant from the range of expected values given above.

It is not very meaningful to make comparisons between estimates of standing crop of phy-

toplankton carbon, such as those given above, and the available data on rate of production of plant carbon. The basis for the estimates of standing crop is imperfect and most of the production data (Table 4) were obtained under nonnatural conditions of constant illumination. As a matter of interest, there are two noon stations in the AB–11 and AB–8 series, numbers 56 and 62 of Table 1, A, for which data are available for primary production rate measured by the more trustworthy *in situ* method, over the water column 0–100 m. The values are respectively 134 and 290 $mgC/m^2/day$ (Blackburn et al., 1962, Appendix I); the corresponding estimated standing crops of phytoplankton for those stations (again using Strickland's factor 30 to multiply weights of chlorophyll *a*) are 1080 and 870 mgC/m^2.

The difference in range of sampling depth for the three standing crops has been noted in the preceding part of the discussion. As shown earlier, the depth was approximately 0–100 m for chlorophyll *a*, 0–300 m for zooplankton (including copepods), and 0–90 m for carnivorous micronekton. Zooplankton hauls over 0–300 m have long been standard in eastern tropical Pacific investigations, in order to minimize effects of diurnal vertical migration. Data in Appendix I show that the great bulk of zooplankton at 0–300 m is actually located at 0–140 m in the eastern tropical Pacific. All standing crop measurements given in Tables 1 and 2 are, therefore, based wholly or mainly on material drawn from a water column or layer between 0–90 m and 0–140 m, with a few exceptions noted elsewhere.

Duration and Maintenance of Possible Steady State

Assuming that the standing crops of the AB–11–Z and AB–8–H data series are in steady-state conditions, the question arises as to the minimum period of time over which these conditions prevailed. This would be about the average time taken for phytoplankton material to be converted into tissue of small primary carnivores (ca. 1–10 cm), but the actual time is unknown. Blackburn (1963) assumed a period of three months in a neighboring area of the eastern tropical Pacific, and was thereby able to relate a series of seasonal changes in properties from wind velocity to abundance of tuna. This does not justify the three-month estimate, but in fact the estimate is not unreasonable; for the Gulf of Panama, Forsbergh (1963) estimated that about two weeks might suffice for herbivores to grow from eggs to adults, and Howard and Landa (1958) showed that a small pelagic fish grows to a length of about 5 cm in between two and three months. The supposed steady-state revealed by the standing crop data in the above-mentioned series of station-pairs may therefore be considered to have lasted at least from late February to late May, when the observations were made; it could have begun earlier, ended later, or prevailed all year.

The data, then, are consistent with a steady balance between plants, herbivores, and primary carnivores, during the northern spring and possibly longer, in most of the area east of 95°W between 12° and 5°N (except the Costa Rica Dome). It might be asked how such a balance can be reconciled with the rather high standing crops and productivity observed, and other signs of biological richness such as the thick oxygen-poor layer that occurs at depth in the area (Wyrtki, 1962, and references cited there). The question arises because Cushing (1959*b*) thought such biological richness in tropical areas would be seasonal, as a result of upwelling, and therefore "unbalanced" as in higher latitudes. Seasonal upwelling does not seem to explain the observations put forward here; it does occur in the northern winter and spring on the continental shelf in the Gulf of Panama (Schaefer et al., 1958), well to the north of A16 and A17 in Figure 2, but this paper does not deal with that area.

Both Cushing (1959*a*, *b*) and Dunbar (1960) considered other ways by which a regular supply of nutrients might be maintained in the tropical euphotic layer, such as regeneration through excretion by animals, but apparently did not consider them sufficient to maintain steady-state conditions in rich areas. This seemed to leave only upwelling, which Cushing thought would be seasonal, at least in its effects upon biota (the standing crop of phytoplankton temporarily restricted by turbulence, then increasing

with the crop of herbivores lagging behind, etc.). There are other possibilities in the part of the eastern tropical Pacific under consideration, however.

According to Cromwell (1958) and Wyrtki (MS, with more abundant data) the region mentioned above is characterized by a very shoal thermocline at all times of year. The mean depth of the mixed layer is <30 m in all months, except in the southwest corner of the region (near A11 and A14, see Fig. 2) where it is >30 m (occasionally >40 m <50 m) from about August through January, and in the northwest corner (west of A13) where it is >30 m in January and February. It is <20 m in large areas of the region from about March through June, although only in small areas near the Costa Rica Dome from about October through December. It is sometimes <10 m, even in areas outside the Costa Rica Dome, and was so observed in the neighborhood of A16 at the time this station-pair was occupied in May, 1958 (Blackburn and associates, 1962, Fig. 9); a similar situation was found in about the same area in March, 1941 (Wooster, 1959, Fig. 15).

Nutrient concentrations are high in and just below the thermocline in this area (Wooster and Cromwell, 1958). As a result, nutrients are always available in the lower part of the euphotic layer, and can be supplied to the upper part of it by vertical mixing caused by wind. Such mixing probably would not carry phytoplankton below the compensation depth. Blackburn (1962) showed that gales could stir the upper part of such shoal thermoclines so as to enrich the mixed layer; the mixed layer was deepened from about 20 m to 30 m, but the thermocline was not destroyed.

The area under consideration is not very windy. No part of it has more than 20% of surface wind above force 4 Beaufort (11–16 knots) in any month, or more than 10% above force 4 in any month from March through July (Meteorological Office, London, 1956). It will be observed that winds are weakest and the mixed layer thinnest from March through July, and a little stronger and thicker during the rest of the year, as might be expected. It seems reasonable to suppose that these waters are stirred to greater than the average depth of the mixed layer when winds of above-average velocity occur, and that this process, probably intermittent, is sufficiently regular to maintain moderate nutrient concentrations in the mixed layer during most of the year.

A steady process of upwelling might have a similar effect, and the following observations by Wyrtki (unpublished) indicate the possibility of such a process occurring in the region of interest. There is an excess of precipitation over evaporation, and so an influx of high-salinity water must occur to maintain the surface salinity at the observed levels. Such water is present below the thermocline, and some of it, therefore, probably ascends.

In any event, surface concentrations of 0.50 $<PO_4$–P <1.00 μg–atm/l. occur in a large part of the area of interest, and concentrations >0.25 <0.50 occur in the remainder of it, and these are moderately high concentrations for tropical Pacific surface waters (Reid, 1962). It appears, therefore, at least qualitatively, that a supply of nutrients can be made available to the euphotic zone in sufficient amount and with sufficient regularity to maintain steady-state conditions among the fairly high standing crops of biota in the region studied.

Nothing definite can be said about the possible effects of horizontal circulation of water in maintaining or opposing steady-state conditions in the region. Information is available on mean monthly direction and velocity of surface currents (Cromwell and Bennett, 1959), and the annual range of variation in direction has been summarized in a useful chart (Schaefer, 1962, Fig. 15). On the whole the current pattern is rather stable from month to month, except in an area between Costa Rica and Cocos Island (including A14 and A15 of Fig. 2), and it is quite possible that the effects of currents in transporting nutrients or biota are sufficiently constant over long periods to permit a steady state to exist.

The foregoing observations on physical features indicate that steady-state conditions might last all year instead of merely in the northern spring. If this were so, standing crops would probably not change much from season to season at any one place in the region of interest, although small gradual changes might occur. Un-

fortunately, insufficient data are available for comparing properties at different seasons, from this part of the eastern tropical Pacific or most other parts. The four cruises which yielded observations of the desired kind in the region between 5° and 12°N and between 95°W and the coast, were Eastropic, Scope, Scot, and Costa Rica Dome. On Scope and Costa Rica Dome the effort was concentrated in particular localities like the Costa Rica Dome, but on Eastropic and Scot it was spread rather evenly over large parts of the area. The Eastropic observations were made in November, 1955 and the Scot observations in May, 1958, and these two sets of data provide a little information about possible seasonal changes in surface chlorophyll *a* and in zooplankton at 0–300 m (Holmes et al., 1957; Holmes and Blackburn, 1960). Surface chlorophyll *a* averaged 0.28 mg/m^3 for 14 Eastropic stations and 0.29 mg/m^3 for 11 Scot stations. Zooplankton (small organisms) averaged 175 ml/10^{3}m^3 for 35 Eastropic stations and 128 ml/10^{3}m^3 for 24 Scot stations (both day and night observations included). Surface PO_4–P, which is also of interest, averaged 0.53 μg–atm/1. for 18 Eastropic stations and 0.34 μg–atm/1. for 11 Scot stations (Scripps Institution of Oceanography, 1962; Holmes and Blackburn, 1960).

This meager information suggests that no great change occurs in standing crops of biota or nutrients between one of the calmer and one of the windier months, and therefore does not deny the possibility of a steady state existing all year round. It was noted previously that the chlorophyll *a* and zooplankton standing crops for 5 Northern Hemisphere autumn stations conformed to the relationship indicated for the AB–11–Z series; all these were in the above-mentioned region of apparent steady-state, as shown in Figure 1, although several other stations from the same series in the same region did not conform in the same way. C and Z were correlated (+0.760, significant at the 1% level) for the 11 stations of the Northern Hemisphere autumn series (Table 2) which were in the steady-state region but not adjacent to the Costa Rica Dome.

No explanation is offered for the fact that all standing crops at a few scattered stations, west and northwest of the apparent steady-state region, conform with the relationships of the AB–11–Z or the AB–8–H series or both; these are A7, B6, and B9, among the northern spring station-pairs (Fig. 2), and D5, D10, and D11 among the northern winter pairs (Table 1, D and Fig. 1). It is worth noting that no such conformity, or any indication of steady-state conditions, was found on any cruise in Baja California (west coast) or the Gulf of Tehuantepec; physical, chemical, and biological conditions are known to vary seasonally in these regions, partly as a result of upwelling and similar processes (Reid, Roden, and Wyllie, 1958; Blackburn, 1962). No steady state was evident off the coast of Peru, an upwelling region (Wyrtki, 1963), although the useful biological data are scanty.

It is concluded that standing crops of phytoplankton, herbivores, and primary carnivores can occur off the Pacific coast of southern Central America in ways that are consistent with steady-state conditions, despite the moderately high levels of these crops. Such indications of possible steady-state conditions are lacking for other areas of the eastern tropical Pacific, which does not deny the existence of such conditions in some of these areas. More information is needed about spatial changes and especially about temporal changes in such standing crops in the eastern tropical Pacific.

Since the region off Central America has supported a successful year-round tuna fishery for many years (Martin, 1962), there are grounds for doubting the generalization of Menzel and Ryther (1961), "It is only in the inefficient eutrophic environments which irregularly produce large surpluses of basic food that large and dense populations of fishes can assemble and subsist." Eutrophic regions, including this one, probably are inefficient in the way herbivores utilize phytoplankton, but this and other features of the productive cycle may be regular and stable in some of the regions.

APPENDIX I

A station list by Klawe (1961, Table 1) enables making a comparison between volumes of zooplankton (small organisms, ml/10^{3}m^3) taken in an oblique haul to about 300 m and in a similar haul made immediately afterwards to

about 140 m, for each of 22 stations near the Revillagigedo Islands and 2 near Alijos Rocks (Fig. 1). These data were gathered on the expedition called "Tuna Spawning Survey" in July, 1957. The net and hauling procedures were as described under "Material" in this paper. The two groups of stations were evenly divided between day and night; so there were 12 of each. The published entry for station 7 gives 74.4 ml of zooplankton for the deeper haul and 52.3 ml for the shallower, but a check on the original collections showed that these entries had been reversed.

The least-squares regression of logarithm of volume from the 300 m haul (Y) on logarithm of volume from the 140 m haul (X) was obtained for the 24 stations, after analysis of covariance had revealed no significant difference between the day and night series. This regression is

$$Y = 0.0566 + 0.8009X$$

with standard error of estimate 0.130, and has been used where necessary in this paper to estimate 300 m-haul volumes from 140 m-haul volumes of zooplankton and copepods (see Table 1 and "Material"). The corresponding regression for estimating logarithm of volume of 140 m haul (Y) from logarithm of volume of 300 m haul (X) is

$$Y = 0.2059 + 1.053X$$

with standard error of estimate 0.128, and it was also used where necessary (see "Discussion").

These regressions can be used to obtain some information about the vertical distribution of zooplankton within the upper 300 m. For a range of selected values of concentration (ml/10^3m^3) in either the 0–140 m or the 0–300 m layer, concentrations for the other layer can be estimated. These values can be used to estimate actual volumes (milliliters) simultaneously present at 0–140 m and 0–300 m under 1 m^2 of sea surface, which may be called a and b. The ratio a/b is quite high even for very low concentrations (e.g., 65% where the 0–300 m concentration is 7 ml/10^3m^3), and it becomes 100% where the 0–300 m concentration is 42 ml/10^3m^3. These calculations are to some extent unrealistic, for obvious reasons; e.g., b–a, representing actual volume at 140–300 m, becomes negative at concentrations higher than those above. They strongly suggest, however, that most of the zooplankton captured in 0–300 m hauls in the eastern tropical Pacific is located in the 0–140 m layer, especially in areas of average and high concentrations, either by day or by night.

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